Observations on the Behavior and Activity of Lobsters, *Homarus americanus*, in Nature

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ABSTRACT

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Observations by means of SCUBA diving on lobsters under natural conditions in Bonavista Bay, Newfoundland, revealed that they undergo a seasonal movement to deeper water in autumn and a return to shallow water in spring and early summer. These movements are not extensive enough to be considered a seasonal inshore-offshore migration. The gradual move to deeper water in autumn appears to be mainly in response to increased turbulence due to storm conditions at this time and the return to shallower water in spring results mainly from increased activity due to increasing temperatures and random movement to shallower, warmer water where they tend to remain.

Nocturnal activity was low at dusk but the peak level appeared to be reached within 2-3 hours after darkness. There was very little activity during the hour before dawn but it was not clear from the observations if activity continued at a high level throughout most of the period of darkness and dropped very quickly or if it tapered off gradually to the very low pre-dawn level.

Territorial behavior varies seasonally with lobsters being virtually non-transient or resident during the winter because of inactivity and much more transient during the summer. Even during summer both types of territorial behavior are present. Lobsters seem to prefer certain shelters which they occupy for varying periods and to which they return by means of a homing ability after varying periods of absence.

Key words: lobsters, seasonal movements, nocturnal activity, territorial behavior, homing

RÉSUMÉ

Ennis, G. P. 1983. Observations on the behavior and activity of lobsters, Homarus americanus, in nature. Can. Tech. Rep. Fish. Aquat. Sci. 1165: v + 26 p.

Des observations menées en plongée sur des homards vivant dans des conditions naturelles dans la baie Bonavista (Terre-Neuve) ont montré qu'ils se déplacent vers les eaux profondes en automne et retournent aux eaux peu profondes au printemps et au début de l'été. Ces déplacements ne sont pas assez importants pour qu'on les qualifie de migration saisonnière entre les zones côtière et hauturière. Il semble que ce mouvement graduel vers les eaux profondes à l'automne soit principalement la conséquence d'une turbulence accrue causée par les tempêtes; le mouvement contraire au printemps découle

surtout d'un accroissement de l'activité attribuable à une augmentation de la température et d'un déplacement erratique vers les eaux chaudes peu profondes où les homards ont tendance à rester.

Durant l'étude, l'activité nocturne était peu élevée au crépuscule, mais le niveau de pointe semblait se produire 2 ou 3 heures après la tombée de la nuit. Peu d'activité a été notée une heure avant l'aube et les observations n'ont pu préciser si l'activité s'est poursuivie à un niveau élevé pendant preque toute la période d'obscurité avant de chuter ou si elle a diminué graduellement jusqu'au faible niveau constaté avant l'aube.

Le comportement territorial varie selon la saison; ainsi, les individus restent pratiquement à la même place pendant l'hiver, période d'inactivité et ils se déplacent beacoup plus en été. Même pendant cette dernière saison, les deux types de comportement territorial existent. Le homard semble préférer certains abris, qu'il occupe pendant des durées variables et qu'il réintégre après une certaine période d'absence, grâce à sa capacité de retour.

INTRODUCTION

Lobsters, Homarus americanus, are accessible to direct observation in nature by means of SCUBA diving. This method of observation is contributing to knowledge of various aspects of their natural behavior and activity (Weiss 1970; Stewart 1970, 1972; Cooper et al. 1975; Cooper and Uzmann 1977, 1980). The seclusive, shelter seeking behavior (Cobb 1971) and the resulting rocky bottom habitat preference of the lobster (Wilder 1958; Scarratt 1968; Cooper and Uzmann 1977, 1980) are well known and are important factors in restricting its local distribution, although lobsters are not entirely absent in soft bottom areas (Thomas 1968; Cooper and Uzmann 1977, 1980). In coastal areas they are essentially non-migratory and tend to form more or less local populations (Wilder 1963a; Cooper 1970; Morrissey 1971; Fogarty et al. 1980).

The present study deals with various aspects of the natural activity and behavior of lobsters within a relatively isolated, local population and includes observations by means of SCUBA diving on seasonal changes in activity and distribution, nocturnal activity and behavior, and territorial and homing behavior.

MATERIALS AND METHODS

In the St. Chad's area of Bonavista Bay, on the northeast coast of Newfoundland, the shoreline is characterized by low to medium height (5-15 m) rocky cliffs. These have provided abundant rock fragments of various sizes and angulations to form a talus slope to depths of about 25 m or more which forms and supports good lobster habitat in terms of shelter and food supply. Over most of the area the bottom slopes steeply from the shoreline so that the deep edge of the talus at about 25 m lies roughly between 45-75 m from shore. Beyond this the bottom consists of a highly calcareous sandy mud and usually slopes more gently.

SCUBA diving was carried out in this area on a year-round basis from September 1967 to March 1970. On each dive a vertical, zig-zag swimming pattern was maintained along the bottom from shallow to deep water and depths at which lobsters occurred were recorded from good quality diver depth guages which were determined to be accurate within .25 to .30 m. All depths were adjusted to normal high tide level. Whenever it was relatively easy to do so, lobsters were removed from their shelters and observations on size and sex were recorded.

In one small section of this area, occupying about 0.4 km of shoreline, 127 lobster shelters were marked and numbered and throughout the period 167 lobsters were marked with colored lobster claw bands (Wilder 1961) around which colored tape was wound. These were pushed over the propodus and dactyl of the claw to the carpus. Different combinations of colours were used so that individual lobsters could be recognized without removing them from their shelters. The lobsters were initially captured in the area while diving both during the day and at night as well as by trapping. Size and sex were recorded and the mark applied, after which they were released in the same area. Much more diving was done in this area where shelters and lobsters were marked than

elsewhere on the grounds. Observations were made on the occupancy of shelters on each dive. Temperatures and light readings (exposure values using a Sekonic Auto-lumi L-86 photo exposure meter pointed towards the surface) were recorded at the surface and on the bottom at 4.6 m depth intervals to 27.5 m. Dives were made at different times from dusk to dawn during May-November 1969. Only one dive was made on any one night but a series of dives was made at different times on consecutive nights. At night an underwater flashlight was used by each diver and observations were made on the number of lobsters in shelters, the number out of shelters and actively wandering over the bottom, the depths at which they occurred and the size and sex of those out of shelters.

RESULTS

SEASONAL CHANGES IN DEPTH DISTRIBUTION

The depth distribution of lobsters changed seasonally (Fig. 1). Winter (December-March) and summer (June-August) depths were significantly different. T-tests gave $P < .01$ for both 1968 and 1969 data. During the summer months, lobsters were generally restricted to a narrower depth range in shallower water than in winter. Starting around late September-early October there was a gradual downslope movement to deeper water where lobsters that moved stayed throughout the winter. Some lobsters, however, remained in shallow water throughout the winter and the winter depth range almost completely overlapped the summer depth range. Starting around late April-early May there was a gradual upslope movement to shallower water. Size (CL) and sex were obtained for 137 of the 248 lobsters observed during winter (December-March 1968-69) and for 43 of the 188 observed during summer 1969. No significant correlations were found between size and depth for either sex during either period. The highest correlation coefficient obtained was .2170 ($.05 < P < .1$) for males during the winter period.

The main barrier to downslope movement during the summer was a fairly strong thermocline that was usually present between 5-10 m (Fig. 2A). The downward movement during the fall appeared to be in response to heavy turbulence in shallow water resulting from stormy weather that becomes more and more common at that time of year. This downward movement is facilitated by the destruction of the thermocline resulting in more or less uniform temperatures throughout a wide depth range (Fig. 2B). This reaction was occasionally seen when storms occurred during the summer such as in late August 1968 (Fig. 1 and 2A). However, in this case there was a return to shallow water shortly afterwards. Decreasing activity resulting from the continuing temperature drop throughout the fall (Fig. 2B) tends to keep the lobsters in deep water and almost complete inactivity because of very low temperatures (Fig. 2C) tends to keep them there throughout the winter. As temperatures rise during the spring (Fig. 2D) activity increases. Storms are common during the spring also and the thermocline is frequently destroyed (Fig. 2D) resulting in more rapid warming of the deep water. The upward movement during the spring results mainly from random wandering into shallower water where the lobsters tend to stay as a more stable thermocline develops in early summer (Fig. 2A). The commercial lobster fishery starts April 20 in this area and even then traps tend to be placed in the shallow end of the lobster's depth range. It is possible that abundant

fresh bait on the grounds may attract lobsters to shallow water. Light readings revealed no seasonal pattern of changes in light conditions (light intensity during daytime) on the grounds that would likely influence these movements.

NOCTURNAL ACTIVITY AND BEHAVIOR

The level of nocturnal activity varied with time of night and seasonally. Throughout this study there were very few observations of lobsters active (out of shelter) during daytime. There was very little activity at dusk but lobsters started to become active soon after darkness occurred (Fig. 3). When a series of dives was made at different times at night during a period of several days, the greatest level of activity was usually reached within 2-3 hours after darkness and remained high for at least another 2-3 hours. There was relatively little activity during the hour before dawn but it was not clear from the data if activity continued at a high level throughout most of the period of darkness and dropped very quickly or if it tapered off gradually to the very low pre-dawn level.

The nocturnal activity index varied with temperature throughout the period July-November (Fig. 4). The level of nocturnal activity was low in early July even compared to that observed on two dives made earlier in the year. This is probably related to reduced feeding activity in the later stages of the intermolt cycle (Weiss 1970). Activity increased during July as did temperature. There was a 2½ week gap in the data in early August but near the end of August activity was at about the same level as at the end of July. The level of activity started to decline in early September and continued to do so throughout the fall. This tapering off in activity corresponded with declining temperatures during the same period. The highest activity index recorded in the main study area (i.e. where shelters were marked) was 0.55 (ie., slightly more than half the total number of lobsters seen on the dive were out of shelters and actively moving over the bottom). When dives were made outside this area, where the bottom and the location of lobster shelters were considerably less familiar, the index was higher (Fig. 4). The reason for this is that in the main study area, the search pattern was not random. Outside this area it was much easier to find lobsters that were out of shelters and actively moving over the bottom whereas in the main study area it was easier to find the lobsters that were in shelters. A true unbiased index would probably be somewhere between those obtained from these two different situations at the same time.

The present observations are inadequate to determine the probably very subtle effects, if any, on nocturnal activity of variations in factors such as tide, weather, turbulence, phase of moon, etc., as well as size and sex of lobster. With respect to size, the smallest nocturnally active lobster of each sex seen were a male 44 mm (carapace length) and a female 46 mm.

TERRITORIAL AND HOMING BEHAVIOR

Only 25% of the lobsters marked within the study area were observed 5 or more times and 46% were not seen after being marked. This indicates that lobsters were moving into and out of the area more or less continuously. Observations on individual lobsters demonstrated considerable variability in territorial behavior. Some lobsters were observed within the study area over extended periods (18 months was the longest) and others for relatively short periods (less than one month) (Table 1). Some were observed repeatedly in just one shelter whereas others were observed in several different shelters. One lobster was seen 45 times over a 9 month period always in the same shelter (Table 1; see also example 13, Appendix 1), although over the period the shelter was sometimes unoccupied or occupied by a different lobster. On the other hand, another lobster was seen in seven different shelters over a 2 month period and still another was seen only 8 times over a 10 month period but each time in a different shelter (Table 1). Quite often, when a lobster was seen in several different shelters over a period of time, there was one shelter that it occupied much more frequently than the others (Table 1).

The longest periods of apparently continuous occupancy of a particular shelter by the same lobster that were recorded were 159 days for one lobster seen 15 times between November 5, 1968 and April 13, 1969 and 160 days for another seen 21 times between December 14, 1968 and May 23, 1969 (see examples 5 and 13, Appendix 1). This latter lobster was also seen, in the same shelter as during the preceding period, 22 times between June 16, 1969 and July 25, 1969. This was the longest period (40 days) of continuous occupancy recorded during summer months. These observations pertain to daytime checks on different days during which these shelters were always occupied by the same lobsters and, over the periods in question, these lobsters were seen in no other shelters.

The number of times that individual shelters were checked for occupancy and the period of time over which these observations continued were highly variable. Over 60% of the marked shelters (Fig. 5) were checked fewer than 10 times or over periods less than one month. The longest period over which observations continued on a given shelter was 30 months. This shelter was checked for occupancy 118 times which is the greatest number of times that a given shelter was checked (Table 2). There was wide variation in the proportion of time that individual shelters were occupied. For shelters that were checked repeatedly over periods of one year or more, (Table 2), the frequency with which they were occupied ranged from 24 to 75% of the times they were checked. Different lobsters occupied these shelters for varying periods. The number of different lobsters per month of observation (Table 2) ranged from .11 to .77. Some shelters observed over periods less than one year had higher averages. Seven different lobsters were seen in one shelter over an 8 month period and three were seen in another over a period of 1.5 months. The greatest number of lobsters observed in any one shelter was 21 (Table 2).

There was some indication of possible competition between lobsters for individual shelters. For example, sometimes a shelter that was occupied at sometime during the night was occupied by a different lobster the following day (Appendix 2, example 1). However, there were no observations of any

aggressive behavior associated with competition for shelters. In an area such as the one where this study was carried out, where there were many more suitable shelters available than there were lobsters, such intraspecific competition would certainly be minimal. On only one occasion were more than one lobster seen together in the same shelter (Appendix 2, example 3). This occurred during the molting period and parts of a recently molted shell were scattered over the bottom near the shelter. The lobsters were probably involved in the mating process. Six days later the shelter was occupied by one lobster. Rock crabs, Cancer irroratus, frequently occupied lobster shelters for short periods and occasionally eelpouts, Macrozoarces americanus, were seen to occupy lobster shelters more or less continuously for periods up to 2½ months. However, there were no observations of any aggressive behavior associated with interspecific competition for shelters.

Throughout the study there were 38 observations of individual lobsters returning to certain shelters after periods of absence in excess of one day. Although the "home" shelters were checked for occupancy repeatedly during the observed periods when these lobsters were absent, in many cases there were lengthy periods between checks during which lobsters could have returned and left again. The observed periods of absence ranged from two days up to a possible 222 days. Fifteen of the 38 observations were for periods of possible absence in excess of 30 days and nine of the other 23 observations were for periods in excess of 15 days. On nine occasions during these periods of absence the lobsters were observed in other shelters within the study area. These shelters ranged from less than 5 to 84 m from the "home" shelter. The "home" shelters were quite often occupied by different lobsters for varying periods during these periods of absence.

Five homing events were recorded for one lobster (see example 10, Appendix 1 and example 3, Appendix 2). It returned to the same shelter after periods of absence that ranged from two to a possible 65 days. Four homing events were recorded for each of the two other lobsters (see examples 4 and 9, Appendix 1 and example 1, Appendix 2). These returned to the same shelter after periods of absence from two to a possible 21 days in one case and from three to a possible 222 days in the other. Three homing events involving two different shelters were recorded for each of two other lobsters (see example 3, Appendix 1) and there were five shelters for which homing events by two different lobsters were recorded (see examples 1 and 3, Appendix 2). One homing event recorded illustrated the seasonal movements to and from deep water (see example 1, Appendix 2). The lobster was seen several times during the autumn (the last time being November 9, 1967) in a shelter at 11.9 m. It was seen November 15, and several times afterward, in a shelter at 27.4 m where it apparently overwintered. On May 9, 1968 the lobster was seen back in the same shelter at 11.9 m.

During night dives it was common to find individual shelters unoccupied that had been occupied during the preceding day and again the following day by the same lobster. This clearly demonstrated that lobsters quite often return to the same shelter following nocturnal wandering, however, there appears to be considerable seasonal variation in the extent to which this occurs. From mid December to mid May, of the shelters checked on two consecutive days that were occupied by a lobster on one or both days, only 4.8% were occupied one day and

not the next or occupied by different lobsters each day (Table 3). Over the remainder of the year this percentage ranged from 28.6% during mid to late May to 62.5% during mid to late September. For the observations presented (Table 3) where the same lobster occupied the same shelter on each of two consecutive days, it is not possible to distinguish between those lobsters that were not active during the intervening night and those that were. The high percentage of shelters occupied by the same lobster on each of two consecutive days during the winter months is more a reflection of a very low level of nocturnal activity than it is an indication that the majority of lobsters returned to the same shelter following nocturnal wandering. Over this period, bottom temperatures over the 4.6 m to 27.4 m depth range were close to or below 0°C.

On six occasions during this study, a lobster which was observed in the same shelter on each of two consecutive days was seen out of its shelter during the intervening night. The maximum distance one of these lobsters was observed away from its shelter was approximately 10 m. On 13 occasions a lobster was observed in two different shelters on two consecutive days. The distances between these shelters ranged from 2 to 84 m and all but three were less than 15 m. The maximum distance between shelters within the study area was approximately 240 m (Fig. 5).

An activity index was obtained from observations on the occupancy of shelters on two consecutive days throughout the year. This showed a well-defined pattern of seasonal changes in nocturnal activity (overnight movement between shelters). From early December to about mid May activity is virtually nil (Fig. 6). Observations on individual lobsters and shelters showed, however, that even during the coldest part of the year some movement between shelters did take place (Table 2; Appendix II). In late May lobsters became more nocturnally active and greatest activity was reached around mid August to early September. Activity decreased throughout October and November and the very low winter level of activity was reached again in December.

DISCUSSION

In contrast to lobsters in offshore areas which undertake extensive inshore-offshore migrations and commonly disperse long distances (Saila and Flowers 1968; Cooper and Uzmann 1971; Uzmann et al. 1977), lobsters in coastal areas are non-migratory and tend to remain within localized areas, although some individuals disperse considerable distances (Wilder 1963a; Morrissey 1971; Dow 1974).

Evidently there is considerable variation in the extent of movements within different coastal areas. Templeman (1935) found average distances moved after 9 to 12 months at large ranging from 7.4 to 26.4 km for different tagging sites in the southern Gulf of St. Lawrence. In Bay St. George and Port au Port Bay (2 adjacent bays on the west coast of Newfoundland) average distances moved by lobsters at large more than 9 months were 3.2 and 8.2 km, respectively (Templeman 1940). Wilder (1963b) found an average straight line distance between release and recapture points of 13.5 km for lobsters at large 10 to

12 months in Egmont Bay, Prince Edward Island. However, all but a few lobsters tagged off southwest Nova Scotia were recaptured very close to the point of liberation with the average distance moved being less than 2 km after about 3.5 months at large (Wilder and Murray 1958). Fogarty et al. (1980) found mean distances between release and recovery sites ranging from 5.5 to 10.4 km off Rhode Island.

Lobsters in the St. Chad's area of Bonavista Bay appear to be more localized than lobsters elsewhere and more than 80% of recaptures, many after a year or more, were within 1 km of the area of initial capture and release (Ennis, unpublished data). Lower average temperatures in the area may be partly responsible for this but coastal physiography and bottom topography likely play a role as well. The narrow band of good "lobster" bottom close to shore is frequently interrupted by the very irregular coastline. Headlands in the area present a partial barrier to lobster movements because of generally much greater water turbulence and more steeply sloping bottom that is mainly bare bedrock or very large boulders which, at best, provides poor sheltering bottom for lobsters.

Wilder and Murray (1958) found no evidence of an inshore-offshore movement of lobsters off southwest Nova Scotia, yet Bergeron (1967) found that lobsters around the Magdalen Islands undertake a seasonal inshore-offshore migration of 11-18 km. Cooper et al. (1975) found no seasonal changes in the abundance of lobsters in waters shallower than 24 m in the Boothbay Region of Maine and concluded that either large-scale movements into and out of the shallow inshore fishing grounds do not occur on a seasonal basis or that inshore and offshore movements are occurring simultaneously and uniformly from season to season. The small scale movement to deeper water in fall and return in spring by lobsters on the St. Chad's grounds is not equated with a seasonal inshore-offshore migration. It appears to result from an avoidance response to turbulence in shallow water caused by an increased frequency of storm conditions during the fall combined with changes in activity related to seasonal changes in temperature conditions on the bottom in the near-shore area. Cooper et al. (1975) found a similar response to stormy weather but its occurrence was irregular and apparently did not result in seasonal shifts in depth distribution. Short-term shifts in distribution in response to short periods of stormy weather were also noted in the St. Chad's area during summer.

Observations on nocturnal activity of lobsters in Long Island Sound and Maine reported by Cooper and Uzmann (1977, 1980) were very similar to those presented here. They reported peak nocturnal activity (80-90% of lobsters $\geq$ 45 mm CL out of shelters in July) occurring four to five hours after sunset and a gradual decrease to sunrise when all had returned to shelters. They also reported that low temperatures (-2 to 1°C) appeared to inhibit nocturnal activity. Emergence from shelters appears to be triggered by low light intensity the level of which varies seasonally, a lower light intensity required during winter (Weiss 1970). While the time associated with the return of lobsters to shelters is highly variable, it tends to occur at approximately the same light intensity (Cooper and Uzmann 1980). During the present study lobsters were seen in shelters during the first couple of hours of darkness feeding on animals that they probably had to leave their shelters to find. It

seems quite likely that the duration of nocturnal activity for individuals is related to availability of food. When food is abundant and readily accessible, nocturnal activity in search of food would be of short duration. Observations also indicate variations in the time of starting and in the duration of nocturnal activity by individual lobsters. It also appears likely that individual lobsters are not nocturnally active every night and sometimes do not move out of their shelters during the night. This is probably related to the relative feeding success of the previous nocturnal wandering.

Observations by Stewart (1970, 1972) on the occupancy of marked shelters in a restricted area in Connecticut waters indicate two types of territorial behavior in lobsters - transient and resident. Transient behavior refers to occupying different shelters for short periods and resident behavior to occupying the same shelter for an extended period. Observations presented here indicate the same types of behavior in lobsters near St. Chad's, Bonavista Bay. There is obviously seasonal variation in the type of territorial behavior, lobsters being considerably less transient in winter but even in summer there is probably some alternation from one type of behavior to the other by individuals. Lobsters seem to prefer certain shelters which are used repeatedly and to which they return after periods of absence for varying periods. The observations indicate considerable variability in the pattern of territorial behavior within a population and by individual lobsters.

Cooper and Uzmann (1977) report that the range of foraging or dispersal on a given night generally does not exceed 300 m but ranges up to 2000 m. Presumably lobsters return to the same shelters after a night of foraging (or after several weeks of absence) by means of some sort of homing ability. The mechanisms involved in this homing ability, however, are unknown.

It is clear that the behavior and activity of lobsters is strongly influenced by environmental and ecological conditions resulting in considerable variability both within and between areas.

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Table 1. Summary of observations on selected individual lobsters.

Sex and carapace length (mm)	# Times observed	Period	# Different shelters occupied	# Times seen in individual shelters
M50	14	May-June/69	2	13(1)[a], 1(1)
M56	21	Jan.-July/69	1	19(1), 2(?)[b]
M59	8	Aug./68-June/69	8	1(8)
M60	10	Oct./67-May/68	5	4(1), 3(1), 1(3)
M60	6	July-Aug./69	1	4(1), 2(?)
M68	45	Dec./68-Sept./69	1	45(1)
M69	5	May-Oct./69	3	2(2), 1(1)
M69	5	July/69	1	4(1), 1(?)
M69	5	May-Aug./69	3	2(1), 1(1), 2(?)
M71	7	May-June/69	1	7(1)
M71	15	July-Sept./69	1	13(1), 2(?)
M78	9	June/69-Feb./70	4	6(1), 1(3)
M79	14	May-Sept./69	3	11(1), 1(2), 1(?)
M81	7	Oct.-Nov./67	2	6(1), 1(1)
M86	25	Oct./68-May/69	2	18(1), 7(1) (?)
M90	9	July-Nov./69	2	4(1), 3(1), 2(?)
M92	15	Sept./68-Sept./69	8	3(1), 2(1), 1(6), 4(1)
M95	5	July/69	1	5(1) (1),
M102	20	May-Aug./69	4	9(1), 6(1), 4(1), 1
M103	19	May/69-Mar./70	5	6(1), 5(1), 2(1), 1 1(1), 4(?)
M107	5	June-July/69	1	4(1), 1(?) 1(1)
F61	11	Feb.-July/69	6	6(1), 1(5)
F62	38	Sept./68-Aug./69	4	19(1), 8(1), 10(1),
F62	6	Jan.-Aug./68	2	3(2)
F63	6	Oct.-Nov./69	1	6(1)
F67	12	July-Aug./69	2	10(1), 1(1), 1(?)
F69	5	Nov./68-Mar./69	1	5(1) (?)
F71	12	June-Aug./69	7	4(1), 3(1), 1(5)
F73	13	July-Oct./69	5	4(1), 2(2), 1(2), 31(2)
F74	7	June-Sept./69	2	2(1), 1(1), 4(?)
F75	26	Sept./68-Aug./69	6	15(1), 3(1), 2(3),
F76	7	Dec./68-May/69	5	1(5), 2(?)
F77	15	June-July/69	3	13(1), 1(2)
F82	6	May-June/69	2	5(1), 1(1)
F85	10	Sept./68-Aug./69	2	6(1), 1(1), 3(?)
F85	5	Aug.-Nov./69	1	5(1) 1(1)
F86	5	July-Aug./69	3	2(2), 1(1)
F86	30	Oct./68-Mar./70	4	16(1), 8(1), 5(1),
F87	5	Nov./67-June/68	4	2(1), 1(3)
F93	11	Dec./68-May/69	4	5(1), 4(1), 1(2)

[a]: 13(1) lobster seen 13 times in one shelter.
[b]: 2(?) lobster seen twice out of shelter.

Table 2. Summary of observations on selected individual shelters.

Shelter depth (m)	No. times observed	Period (months)	No. times occupied by a lobster	No. different lobsters
8.2	45	24	14	4
4.6	91	20	66	14
7.5	35	22	20	8
11.9	118	30	60	21
7.0	98	20	63	13
12.2	23	18	9	4
12.5	24	15	8	4
14.0	29	14	15	4
12.5	36	15	18	7
7.3	17	10	6	3
7.9	63	15	33	6
11.6	19	14	11	5
6.7	46	13	29	10
7.8	56	15	19	7
7.8	73	13	55	4
8.8	25	14	8	4
14.0	50	14	12	8
8.2	60	15	38	11
8.2	80	19	37	4
12.2	25	15	7	4
13.1	24	19	8	2
13.1	65	13	22	2
8.2	54	15	21	5
9.6	65	29	19	7
15.5	59	19	15	5
10.4	82	19	35	7
8.5	37	17	18	4
7.3	51	15	30	4
9.8	81	19	39	6
27.7	56	19	25	4
17.7	72	25	44	4
9.1	36	14	26	4
11.0	42	15	13	2
10.1	20	13	10	5
27.4	55	19	33	5
7.3	31	14	15	5
12.5	21	13	7	5
11.6	35	14	15	4
8.2	41	10	25	7
7.6	36	6	27	4
7.6	14	2	12	2
9.4	17	1½	11	2
7.3	18	1½	11	3
7.3	33	4	27	4
10.4	26	2	14	1
4.6	19	8	13	7

Table 3. Summary of observations on occupancy of individual shelters on two consecutive days at different times of the year.

Period	Number of Observations[a]	% occupied one day and empty other (#)	% occupied by a different lobster each day (#)	% occupied by same lobster each day (#)
Jan. 14-31	18	22.2 (4)	5.6 (1)	72.2 (13)
Feb. 1-15	19	-	-	100.0 (19)
Feb. 16-28	9	-	-	100.0 (9)
Mar. 1-15	10	-	-	100.0 (10)
Mar. 16-31	11	-	-	100.0 (11)
Apr. 1-15	8	-	-	100.0 (8)
May 1-15	20	-	-	100.0 (20)
May 16-31	35	25.7 (9)	2.9 (1)	71.4 (25)
June 1-15	22	40.9 (9)	-	59.1 (13)
June 16-30	22	45.5 (10)	-	54.5 (12)
July 1-15	49	26.5 (13)	6.1 (3)	67.3 (33)
July 16-31	171	42.7 (73)	2.9 (5)	54.4 (93)
Aug. 16-31	102	58.8 (60)	-	41.2 (42)
Sept. 1-15	38	55.3 (21)	2.6 (1)	42.1 (16)
Sept. 16-30	16	62.5 (10)	-	37.5 (6)
Oct. 1-15	36	58.3 (21)	-	41.7 (15)
Oct. 16-30	10	50.0 (5)	-	50.0 (5)
Nov. 1-16	30	50.0 (15)	6.7 (2)	43.3 (13)
Dec. 1-16	10	-	-	100.0 (10)

[a]: No. shelters checked on two consecutive days that contained a lobster on one or both days

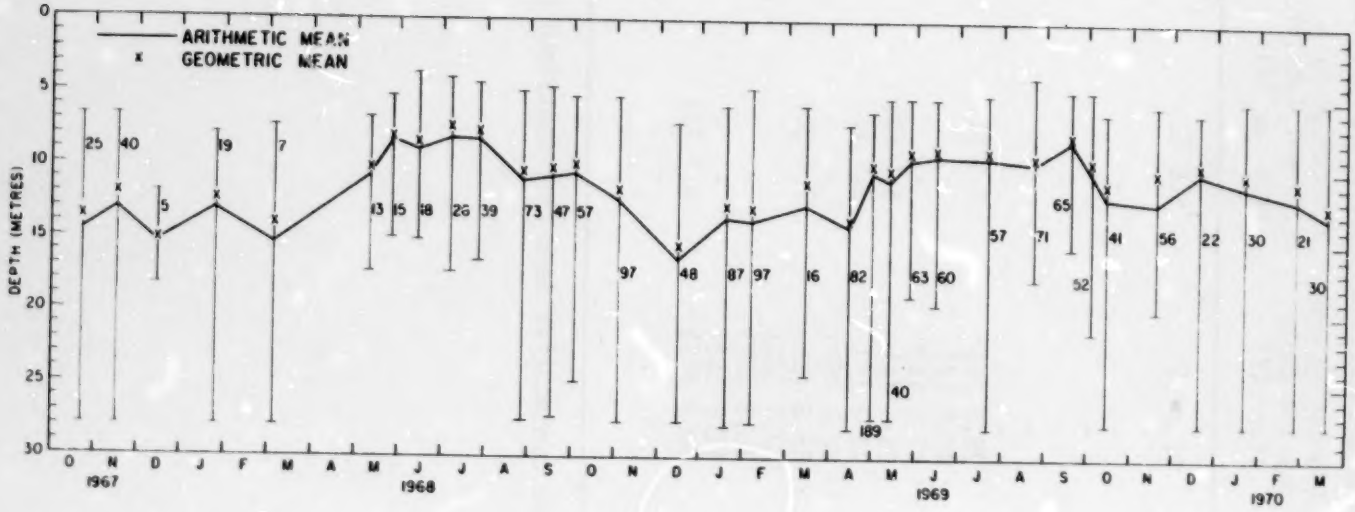

Fig. 1. Seasonal changes in depth distribution of lobsters on the St. Chad's grounds October 1967-March 1970. Vertical lines show range in depth, figure given is number of observations.

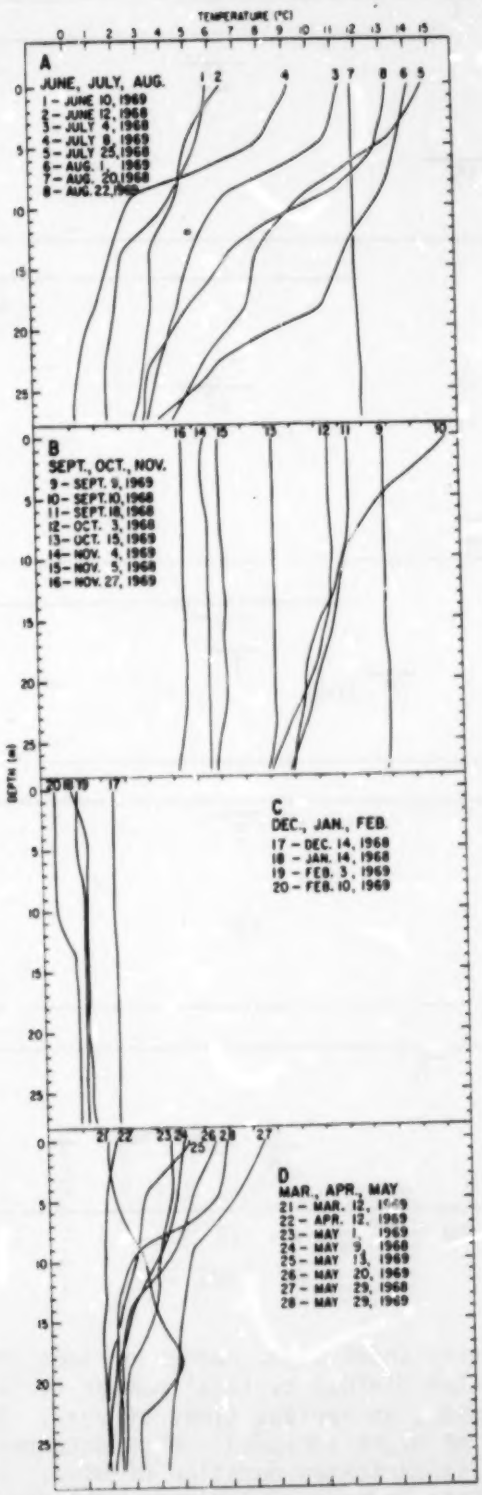

Fig. 2A-D. Depth-temperature profiles for different seasons on St. Chad's lobster grounds.

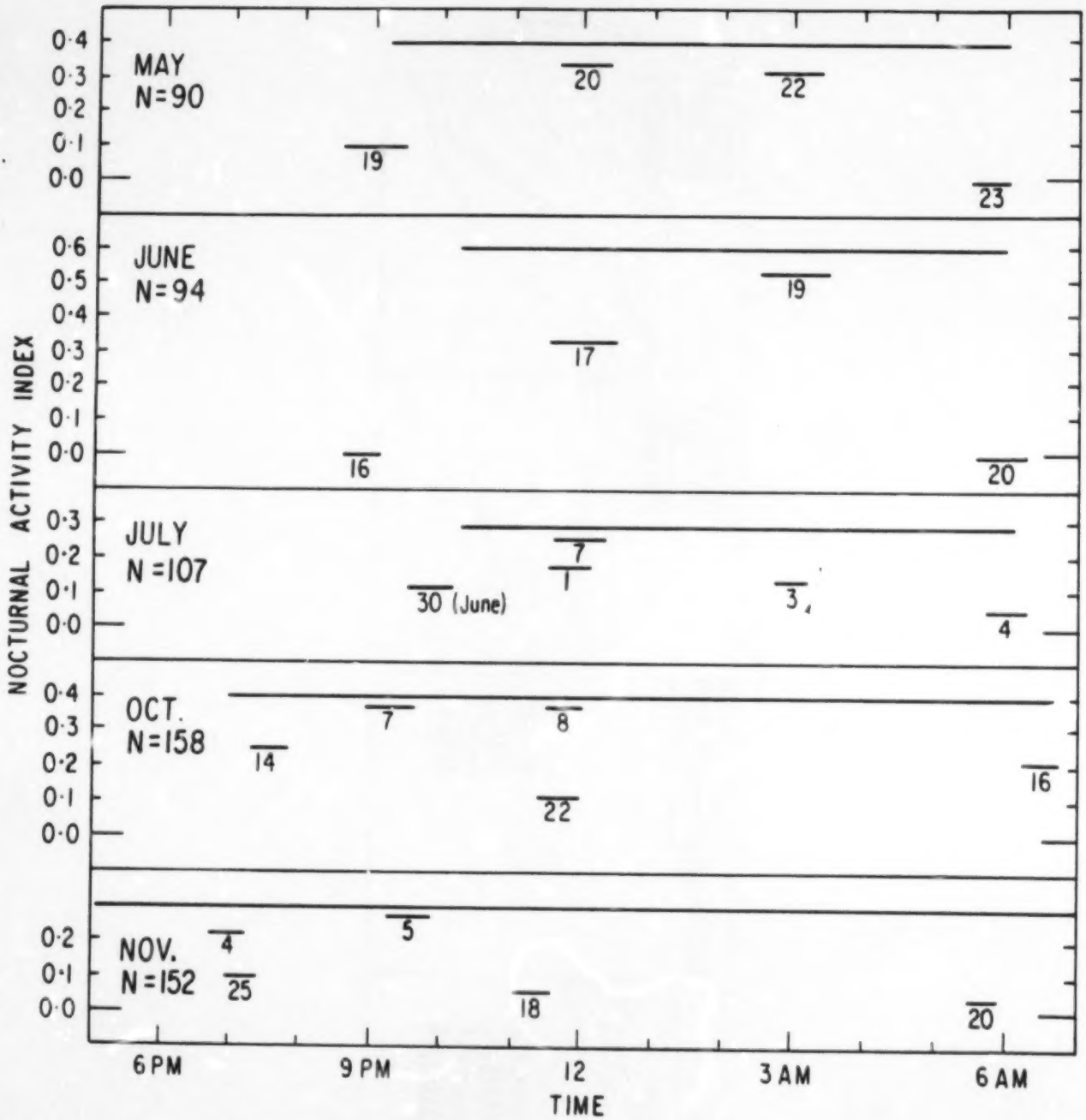

Fig. 3. Nocturnal activity index (i.e. number of lobsters out of shelter and actively moving over bottom divided by total number of lobsters seen on dive) for different times of night at various times of year. Only series of dives done at different times of night included. Each data point is represented by a horizontal line which also indicates duration of dive. Numbers next to data points are dates, N is total number of lobsters seen for all points in each graph. Horizontal line at top of each graph indicates approximate period of darkness.

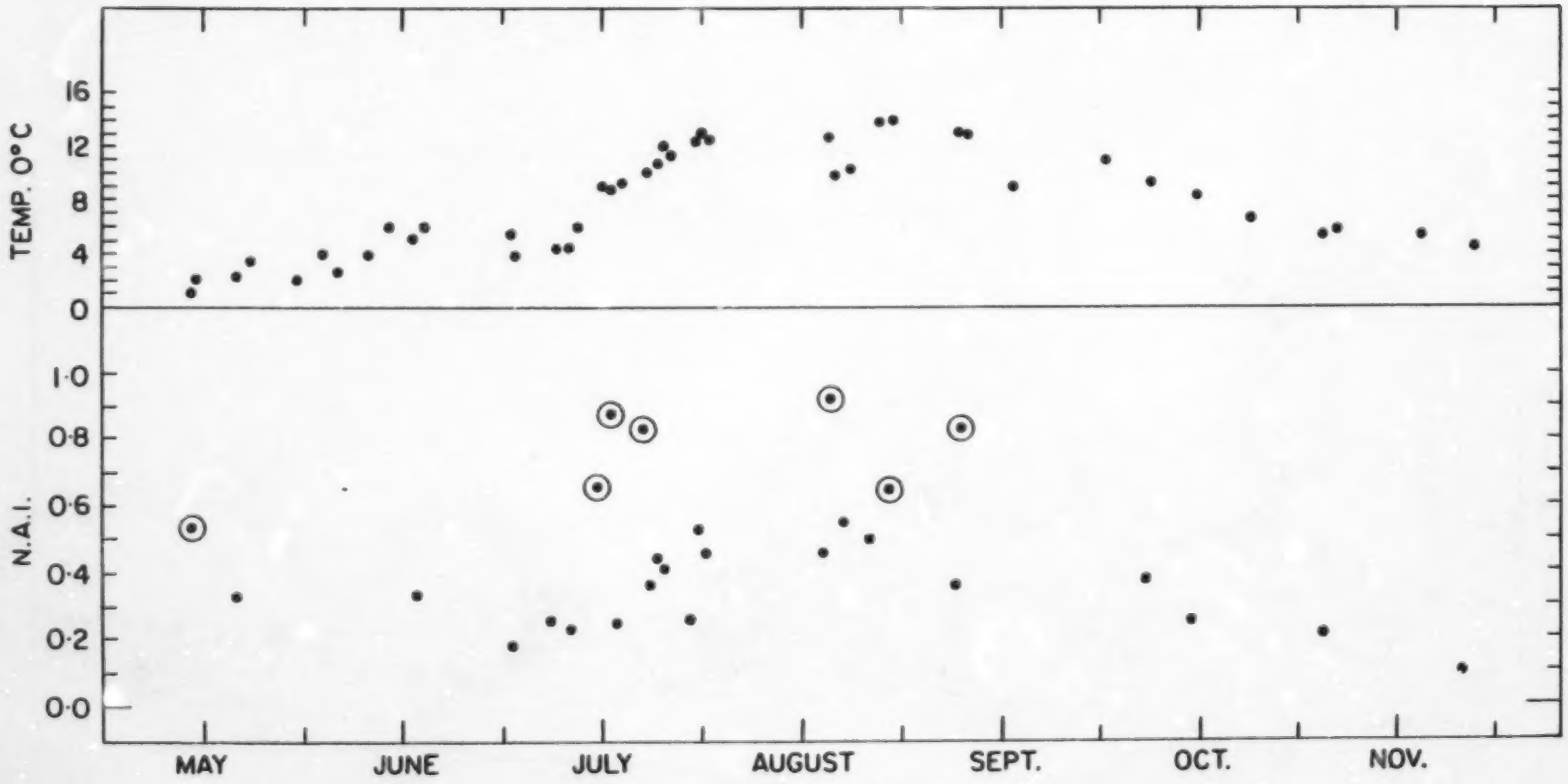

Fig. 4. Average of temperatures on the bottom at 4.6, 9.1, 13.7 m and nocturnal activity index (N.A.I.) for dives within 2-3 h after darkness. Circled points indicate dives made outside the main study area.

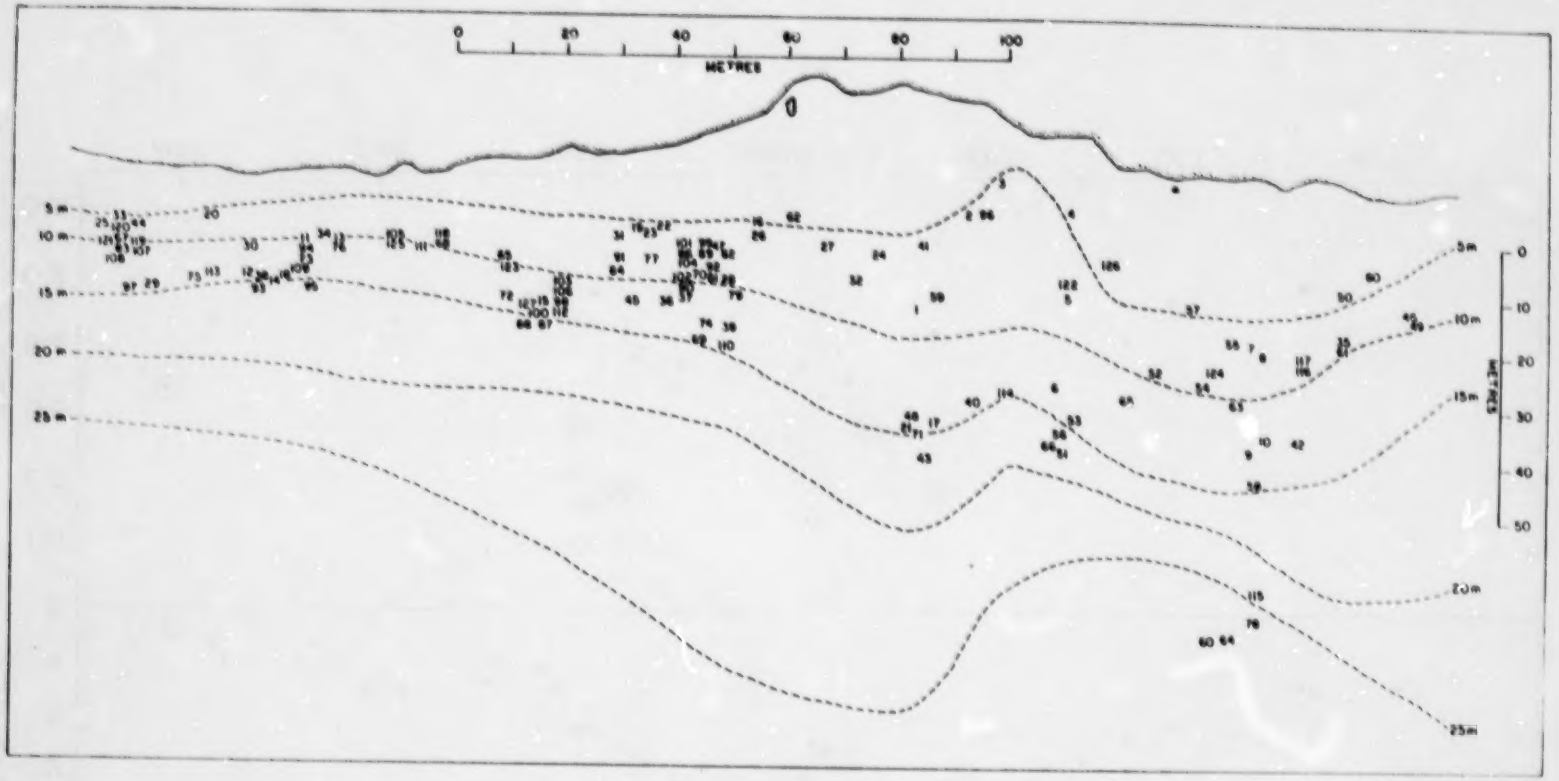

Fig. 5. Main diving area showing depth contours. Figures are shelter numbers which are shown in the location of the shelters within the area.

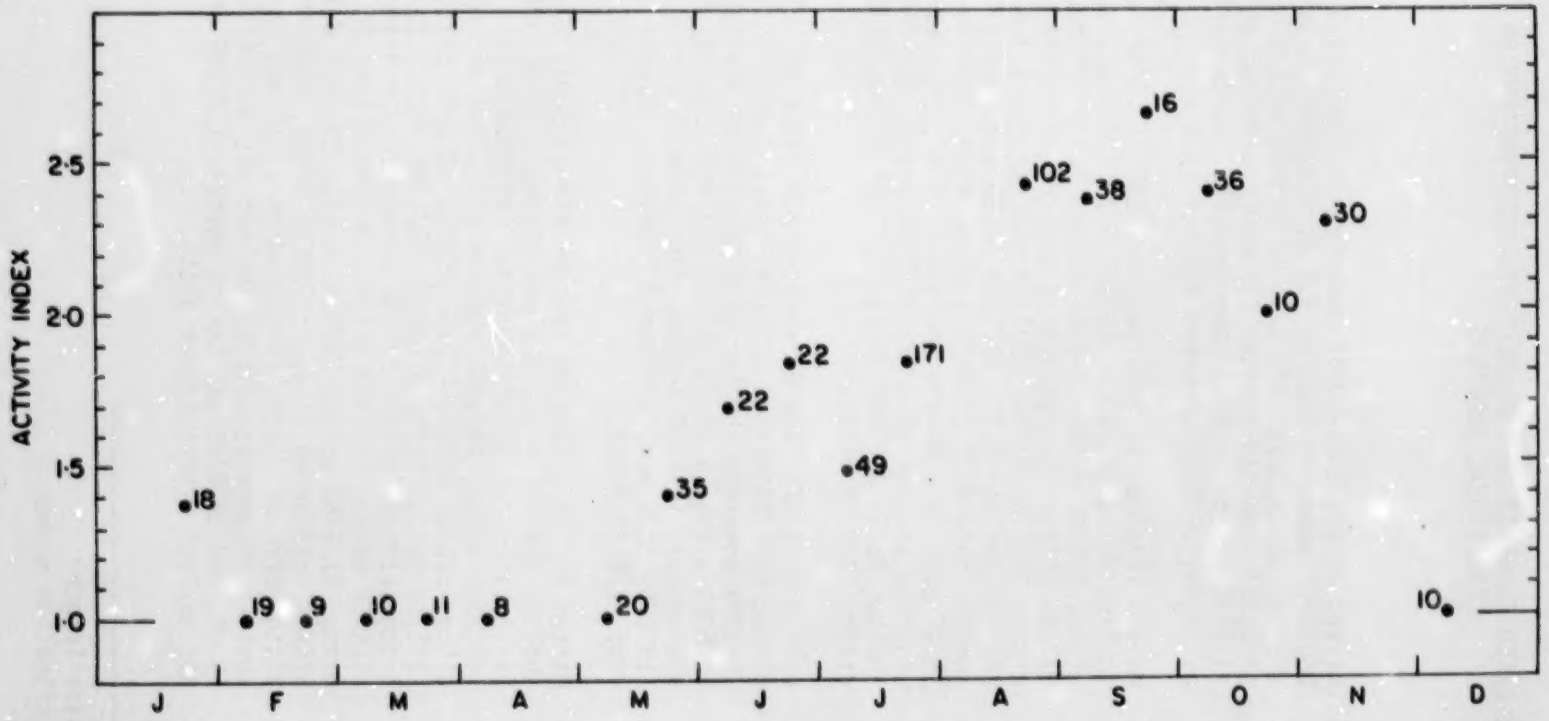

Fig. 6. Seasonal changes in lobster activity index (i.e. number of shelters checked on two consecutive days that contained a lobster on one or both days divided by the number of shelters that contained the same lobster on both days). Figures are number of observations.

APPENDIX 1: SELECTED EXAMPLES OF CHRONOLOGICAL OBSERVATIONS ON INDIVIDUAL LOBSTERS

Example #

1. M60*/#8** - Marked 22/9/67; 19/10/67 unmarked shelter (11.9 m); 26/10/67 unmarked shelter 7.9 m; 27/10/67 in same shelter as on 19/10/67; 1/11/67 ditto; 9/11/67 ditto; 15/11/67 unmarked shelter (27.4 m); 16/11/67 ditto; 23/11/67 ditto; 9/4/68 same unmarked shelter (11.9 m) as above; 29/4/68 unmarked shelter (7.9 m).

2. F75/#56 - Marked 12/9/68; 13/9/68 shelter #103 (11.6 m); 18/9/68 ditto; 30/6/69 shelter #123 (10.7 m); 1/7/69 ditto; 2/7/69 ditto; 3/7/69 ditto; 7/7/69 ditto; 9/7/69 ditto; 10/7/69 ditto; 11/7/69 ditto; 15/7/69 ditto; 16/7/69 ditto; 18/7/69 shelter #15 (12.5 m); 22/7/69 shelter #123; 22/7/69 11:30 p.m. out of shelter near #15; 23/7/69 shelter #123; 23/7/69 11:45 p.m. in unmarked shelter (7.9 m); 24/7/69 in unmarked shelter (9.1 m); 25/7/69 ditto; 28/7/69 in shelter #123; 29/7/69 ditto; 31/7/69 ditto; 18/8/69 ditto; 19/8/69 ditto.

3. M50/#63 - Marked 26/9/67; 19/5/69 shelter #76 (10.4 m); 21/5/69 ditto; 22/5/69 ditto; 23/5/69 ditto; 28/5/69 ditto; 29/5/69 unmarked shelter (9.4 m); 5/6/69 shelter #76; 10/6/69 ditto; 11/6/69 ditto; (13 and 16/6/69 shelter #76 empty); 17/6/69 shelter #76; 18/6/69 ditto; (19/6/69 2:30 a.m. shelter #76 empty); 19/6/69 shelter #76; 20/6/69 ditto.

4. F62/#64 - Marked 26/9/67; 13/9/68 shelter #47 (7.9 m); 29/10/68 shelter #64 (27.4 m); 5/11/68 ditto; 6/11/68 ditto; 14/12/68 ditto; 15/12/68 ditto; 16/12/68 ditto; 18/12/68 ditto; 14/1/69 shelter #78 (27.4 m); 15/1/69 ditto; 3/2/69 ditto; 4/2/69 ditto; 10/2/69 ditto; 11/2/69 ditto; 12/3/69 ditto; 13/3/69 ditto; 12/4/69 ditto; 13/4/69 ditto; 1/5/69 ditto; 2/5/69 ditto; 13/5/69 ditto; 14/5/69 ditto; 19/5/69 ditto; 20/5/69 ditto; 21/5/69 ditto; 22/5/69 ditto; 23/5/69 ditto; 3/6/69 shelter #8 (7.0 m); 5/6/69 ditto; 10/6/69 ditto; 11/6/69 ditto; 13/6/69 ditto; (17 and 18/6/69 shelter #8 empty); 19/6/69 shelter #8; 20/6/69 ditto; (8, 9, and 10/7/69 shelter #8 empty); 11/7/69 shelter #8; 15/7/69 ditto; 1/8/69 ditto.

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* sex and carapace length
** lobster identification number

Example #

5. F86 / #85 - Marked 1/10/68; 3/10/68 in unmarked shelter (4.6 m); 30/ 10/68 shelter #8 (7.0 m); 5/11/68 ditto; 6/11/68 ditto; 14/12/68 ditto; 15/12/68 ditto; 16/12/68 ditto; 18/12/68 ditto; 14/1/69 ditto; 3/2/69 ditto; 4/2/69 ditto; 10/2/69 ditto; 11/2/69 ditto; 12/3/69 ditto; 13/3/69 ditto; 12/4/69 ditto; 13/4/69 ditto; 28/7/69 shelter #126 (4.6 m); 7/10/69 ditto; 8/10/69 shelter #4 (4.6 m); 15/10/69 shelter #126; 22/10/69 shelter #4; 4/11/69 ditto; 5/11/69 ditto; 18/11/69 ditto; 20/11/69 ditto; 25/11/69 ditto; 28/11/69 ditto; 20/1/70 shelter #126; 17/3/70 ditto.

6. M103 / #88 - Marked 2/10/68; 1/5/69 shelter #8 (7.0 m); 2/5/69 ditto; 22/7/69 ditto; 24/7/69 unmarked shelter (7.9 m); 25/7/69 ditto; 30/7/69 shelter #49 (9.6 m); 18/8/69 unmarked shelter (6.7 m); 19/8/69 shelter #8; 20/8/69 ditto; 21/8/69 ditto; 21/8/69 11:30 p.m. out of shelter near #8; 22/8/69 unmarked shelter (8.5 m); 25/8/69 11:30 p.m. out of shelter; 14/10/69 unmarked shelter (11.0 m); 22/10/69 ditto; 4/11/69 ditto; 18/11/69 ditto; 25/11/69 ditto; 17/3/70 ditto.

7. M86 / #96 - Marked 3/10/68; 30/10/68 shelter #61 (9.8 m); 5/11/68 shelter #35 (8.2 m); 6/11/68 ditto; 15/12/68 ditto; 16/12/68 ditto; 18/12/68 ditto; 14/1/69 ditto; 3/2/69 ditto; 4/2/69 ditto; 10/2/69 ditto; 11/2/69 ditto; 12/3/69 ditto; 13/3/69 ditto; 12/4/69 shelter #61; 13/4/69 ditto; 1/5/69 shelter #35; 2/5/69 ditto; 13/5/69 shelter #61; 14/5/69 ditto; 19/5/69 ditto; 20/5/69 ditto; 21/5/69 shelter #35; 22/5/69 2:30 a.m. ditto; 22/5/69 ditto; 23/5/69 5:30 a.m. ditto.

8. M56 / #117 - Marked 5/11/68; 14/1/69 shelter #42 (12.2 m); 11/2/69 unmarked shelter (11.9 m); 13/3/69 shelter #42; 12/4/69 ditto; 13/4/69 ditto; 1/5/69 ditto; 2/5/69 ditto; 13/5/69 ditto; 14/5/69 ditto; 19/5/69 ditto; 20/5/69 ditto; 21/5/69 ditto; 22/5/69 ditto; 23/5/69 ditto; 3/7/69 ditto; 7/7/69 ditto; 9/7/69 ditto; 10/7/69 ditto; 11/7/69 ditto; 17/7/69 11:45 p.m. out of shelter near #42; (18/7/69 #42 empty); 24/7/69 12:10 a.m. out of shelter near #42; (25/7/69 #42 empty).

Example #

9. F71 / #118 - Marked 6/11/68; 16/6/69 shelter #44 (7.9 m); 17/6/69 unmarked shelter (8.8 m) near #44; 19/6/69 shelter #44; 4/7/69 unmarked shelter (7.9 m) near #44; 10/7/69 unmarked shelter (8.5 m); 17/7/69 unmarked shelter (6.4 m); 23/7/69 11:30 p.m. shelter #44; 24/7/69 unmarked shelter (7.9 m) near #44; 29/7/69 shelter #119 (9.4 m); 30/7/69 ditto; 31/7/69 ditto; 18/8/69 shelter #44.

10. M79 / #121 - 13/5/69 shelter #6 (11.3 m); 14/5/69 ditto (marked today); 15/5/69 shelter #31 (7.0 m); 18/7/69 shelter #6; 22/7/69 ditto; 23/7/69 ditto; 23/7/69 11:30 p.m. out of shelter (12.2 m); 24/7/69 shelter #6; 25/7/69 ditto; 29/7/69 unmarked shelter (18.6 m); 30/7/69 shelter #6; 1/8/69 ditto; 25/8/69 ditto; 9/9/69 ditto.

11. M102 / #130 - Marked 20/5/69; 21/5/69 shelter #61 (9.1 m); 22/5/69 2:30 a.m. ditto; 22/5/69 ditto; 23/5/69 ditto; 28/5/69 ditto; 29/5/69 ditto; 11/6/69 shelter #36 (11.6 m); 13/6/69 ditto; 16/6/69 ditto; 17/6/69 ditto; 18/6/69 shelter #111 (10.7 m); 19/6/69 2:30 a.m. ditto; 19/6/69 ditto; 7/7/69 11:35 p.m. ditto; 22/7/69 ditto; 24/7/69 ditto; 28/7/69 ditto; 29/7/69 unmarked shelter (11.3 m); 30/7/69 shelter #111; 31/7/69 ditto; 1/8/69 ditto.

12. M71 / #148 - Marked 19/6/69; 4/7/69 shelter #118 (7.6 m); 9/7/69 ditto; 10/7/69 ditto; 17/7/69 ditto; 22/7/69 ditto; 23/7/69 ditto; 24/7/69 ditto; 25/7/69 ditto; 28/7/69 ditto; 29/7/69 ditto; 30/7/69 ditto; 31/7/69 ditto; 1/8/69 ditto; 18/8/69 11:30 p.m. out of shelter (11.0 m); 8/9/69 11:15 p.m. out of shelter (15.2 m).

Example #

13. M68 #I56 - 14, 16 and 18/12/68 shelter #24 (6.1 m); 15/1/69 ditto; 3,4 and 11/2/69 ditto; 12 and 13/3/69 ditto; 12 and 13/4/69 ditto; 1, 2, 13, 14, 15, 19, 20, 21, 22 and 23/5/69 ditto; (10, 11 and 13/6/69 #24 empty); 16 and 17/6/69 shelter #24; (17/6/69 11:30 p.m. shelter #24 empty); 18/6/69 shelter #24; 19/6/69 2:30 a.m. out of shelter near shelter #24; 19/6/69 shelter #24; 20/6/69 ditto; 30/6/69 ditto; 1/7/69 ditto; 2/7/69 ditto; 3/7/69 ditto; (3/7/69 3:00 a.m. #24 empty); 4/7/69 shelter #24; 7/7/69 11:45 p.m. ditto; 8/7/69 ditto; 9/7/69 ditto; 9/7/69 11:40 p.m. ditto; 10/7/69 ditto; 10/7/69 12:10 a.m. ditto; 11/7/69 ditto; 15/7/69 ditto; 16/7/69 ditto; 17/7/69 ditto; 17/7/69 11:50 p.m. ditto; 18/7/69 ditto; 22/7/69 ditto; (22/7/69 11:45 p.m. #24 empty); 23/7/69 shelter #24; 23/7/69 11:45 p.m. ditto; 24/7/69 ditto; 24/7/69 12:10 a.m. ditto; 25/7/69 ditto; (28, 29 and 30/7/69 #24 empty); 17/9/69 shelter #24.

APPENDIX 2: SELECTED EXAMPLES OF CHRONOLOGICAL OBSERVATIONS ON INDIVIDUAL SHELTERS

Example #

1. (7.0)* #8** - 4/7/68 unmarked lobsters; 24 and 30/7/68 empty; 28, 29 and 30/8/68 same unmarked lobster; 13/9/68 ditto; 16, 18 and 30/9/68 empty; 1/10/68 unmarked lobster; 2/10/68 empty; 3/10/68 unmarked lobster; 30/10/68 lobster #85 (F86); 4, 5 and 6/11/68 ditto; 14, 15, 16 and 18/12/68 ditto; 14/1/69 ditto; 3, 4, 10 and 11/2/69 ditto; 12 and 13/3/69 ditto; 12 and 13/4/69 ditto; 1 and 2/5/69 lobster #88 (M103); 13, 14, 19, 20 and 21/5/69 lobster #128 (F77); 22/5/69 2:30 a.m. lobster #129 (F92); 22, 23, 28 and 29/5/69 ditto; 3/6/69 lobster #64 (F62); 4/6/69 empty; 5, 10, 11 and 13/6/69 lobster #64; 16, 17 and 18/6/69 empty; 19 and 20/6/69 lobster #64; 30/6/69 empty; 1 and 2/7/69 empty; 3/7/69 2:40 a.m. empty; 3/7/69 unmarked lobster; 4, 8, 9 and 10/7/69 empty; 11/7/69 12:10 a.m. lobster #128 (F77); 11/7/69 lobster #64; 15/7/69 ditto; 16, 17 and 18/7/69 empty; 22/7/69 lobster #88; 22/7/69 11:30 p.m. ditto; 23 and 24/7/69 empty; 24/7/69 11:50 p.m. lobster #89 (M90); 25/7/69 ditto; 28, 29, 30, 31 and 31 (11:30 p.m.) /7/69 empty; 1/8/69 lobster #64; 18/8/69 11:30 p.m. empty; 19, 20 and 21/8/69 lobster #88; 21/8/69 11:30 p.m. empty; 22, 26 and 27/8/69 empty; 28/8/69 unmarked lobster; 9, 10, 16 and 17/9/69 empty; 1, 7, 8, 16 and 22/10/69 unmarked lobster; 25/11/69 unmarked lobster; 20 and 21/1/70 unmarked lobster; 25/2/70 empty; 17 and 18/3/70 unmarked lobster.

2. (7.8) #24 - 20, 27 and 30/8/68 unmarked lobster; 10, 12, 13, 16, 18 and 30/9/68 empty; 1/10/68 empty; 3/10/68 unmarked lobster; 29/10/68 empty; 6/11/68 empty; 14, 16 and 18/12/68 lobster #156 (M68); 15/1/69 ditto; 3, 4 and 11/2/69 ditto; 12 and 13/3/69 ditto; 12 and 13/4/69 ditto; 1, 2, 13, 14, 15, 19 and 20/5/69 ditto; 20/5/69 11:35 p.m. empty; 21, 22 (2:30 a.m.), 22 and 23/5/69 lobster #156; 10, 11 and 13/6/69 empty; 16 and 17/6/69 lobster #156; 17/6/69 11:30 p.m. empty; 18/6/69 lobster #156; 19/6/69 2:30 a.m. empty; 19, 20 and

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* shelter depth (m)
** shelter identification number

Example #

2. 30/6/69 lobster #156; 1, 1 (11:30 p.m.), 2, 3 (2:40 a.m.), 3, 4, 7 (11:35 p.m.), 8, 9, 9 (11:40 p.m.), 10, 10 (11:50 p.m.), 11, 15, 16, 17, 17 (11:35 p.m.), 18 and 22/7/69 ditto; 22/7/69 11:30 p.m. empty; 23, 23 (11:30 p.m.), 24, 24 (11:50 p.m.) and 25/7/69 lobster #156; 29/7/69 unmarked lobster; 30 and 31/7/69 empty; 1/8/69 unmarked lobster; 19/8/69 empty; 21/8/69 unmarked lobster; 21/8/69 11:30 p.m. empty; 22/8/69 unmarked lobster; 25/8/69 11:30 p.m. empty; 26, 27 and 28/8/69 empty; 9 and 10/9/69 empty; 17/9/69 lobster #156.

3. (11.9) #6 - 27/9/67 lobster #23 (F62); 28/9/67 empty; 3/10/67 empty; 9/10/67 unmarked lobster; 17/10/67 different unmarked lobster; 19/10/67 different unmarked lobster; 25 and 27/10/67 empty; 1 and 9/11/67 lobster #18 (M83); 15/11/67 empty; 16/11/67 unmarked lobster; 23/11/67 lobster #49; 13/12/67 unmarked lobster; 23/1/68 unmarked lobster; 24/1/68 empty; 25/1/68 lobster #72 (M81); 12/3/68 unmarked lobster; 9/5/68 unmarked lobster; 30/5/68 empty; 12/6/68 empty; 4/7/68 unmarked lobster; 24/7/68 unmarked lobster; 30/7/68 empty; 21/8/68 two unmarked lobsters (probably mating, parts of recently molted shell outside shelter); 27, 29 and 30/8/68 unmarked lobsters; 10, 12, 13 and 16/9/68 unmarked lobsters; 18 and 30/9/68 empty; 1, 2, 3, 29 and 30/10/68 empty; 4/11/68 lobster #113 (F76); 5 and 6/11/68 empty; 14/12/68 empty; 14/1/69 lobster #52 (M92); 15/1/69 lobster #105 (F93); 3, 4, 10 and 11/2/69 empty; 12 and 13/3/69 empty; 12 and 13/4/69 lobster #105; 1 and 2/5/69 ditto; 13 and 14/5/69 lobster #121 (M79); 15, 20, 21, 22 and 23/5/69 empty; 28/5/69 unmarked lobster; 29/5/69 empty; 3, 4, 5 and 10/6/69 empty; 11/6/69 unmarked lobster; 13, 16, 17 and 19/6/69 empty; 1, 3, 4, 8, 9, 10, 11 and 15/7/69 empty; 17, 18 and 22/7/69 lobster #121; 22/7/69 11:45 p.m. empty; 23/7/69 lobster #121; 23/7/69 11:45 p.m. empty; 24/7/69 lobster #121; 24/7/69 11:50 p.m. empty; 25/7/69 lobster #121; 29/7/69 empty;

Example #

3. 30/7/69 lobster #121; 31/7/69 empty; 1/8/69 lobster #121; 19, 21 and 22/8/69 empty; 25/8/69 11:30 p.m. lobster #121; 26 and 27/8/69 empty; 9/9/69 lobster #121; 10/9/69 empty; 16/9/69 unmarked lobster; 17/9/69 empty; 1/10/69 empty; 8 and 14/10/69 lobster #167; 15/10/68 empty; 22/10/69 11:30 p.m. lobster #167; 4, 5, 18, 20, 25 and 28/11/69 ditto; 20 and 21/1/70 ditto; 25 and 26/2/70 ditto; 17 and 18/3/70 ditto.

4. (8.2) #35 - 21 and 28/8/69 empty; 29/8/68 unmarked lobster; 10, 12, 13, 16, 18 and 30/9/68 empty; 2, 3 and 30/10/68 empty; 4/11/68 empty; 5 and 6/11/68 lobster #96 (M86); 15, 16 and 18/12/68 ditto; 14/1/69 ditto; 3, 4, 10 and 11/2/69 ditto; 12 and 13/3/69 ditto; 12 and 13/4/69 empty; 1 and 2/5/69 lobster #96; 13, 14 and 20/5/69 empty; 21, 22 (2:30 a.m.), 22 and 23/5/69 lobster #96; 29/5/69 empty; 4, 5, 10, 11, 13, 16 and 17/6/69 empty; 18, 19 (2:30 a.m.), 19 and 20/6/69 lobster #106; 30/6/69 empty; 1, 2, 3 and 4/7/69 empty; 7 (11:35 p.m.), 8, 9, 9 (11:40 p.m.), 10, 10 (11:55 p.m.), 11, 15, 16, 17, 17 (11:35 p.m.) and 18/7/69 unmarked lobster; 22, 23, 25, 30 and 31/7/69 empty; 1, 19, 22, 26 and 27/8/69 empty; 9/9/69 empty; 10 and 16/9/69 unmarked lobster; 1/10/69 empty; 18/11/69 11:05 p.m. lobster #106; 20/11/69 empty; 21/1/70 lobster #106; 25 and 26/2/70 ditto; 18/3/70 ditto.